ELSEVIER

Neuropsychologia 45 (2007) 1400–1407

NEUROPSYCHOLOGIA

www.elsevier.com/locate/neuropsychologia

Spatial attention and the mental number line: Evidence for characteristic biases and compression

Matthew R. Longo [a,b,c,*], Stella F. Lourenco [a,d]

[a] Department of Psychology, University of Chicago, Chicago, IL, United States
[b] Institute of Cognitive Neuroscience, University College London, London, United Kingdom
[c] Department of Psychology, University College London, London, United Kingdom
[d] Department of Psychology, Emory University, Atlanta, GA, United States

Received 20 April 2006; received in revised form 2 November 2006; accepted 4 November 2006
Available online 8 December 2006

Abstract

Numbers are often proposed to be represented spatially as lying along a *mental number line*. The present study examined whether the direction of spatial attention operates similarly in physical and numerical space. Participants bisected physical lines by indicating the perceived center and "bisected" the mental number line by estimating (without calculating) the number midway between two others. Healthy participants generally show a slight leftward bias (*pseudoneglect*) when bisecting physical lines. In the present study, pseudoneglect was also observed on mental number line bisection and, importantly, was greater for participants who showed stronger pseudoneglect on physical line bisection. This finding suggests that hemispheric asymmetries in spatial attention operate similarly in physical and numerical space. Furthermore, this bias increased with the average of the numbers, consistent with the proposal that the spatial representation of the mental number line is nonlinearly compressive, with pairs of numbers lying closer together as their magnitude increases.

Keywords: Number line; Pseudoneglect; Representational space; Line bisection

1. Introduced

Numbers are often conceived as falling along a *mental number line*. Dehaene (1997) and colleagues have proposed a model of the mental number line with two main features: it is spatially oriented from left to right, at least for English and French speakers (Dehaene, Bossini, & Giraux, 1993; Hubbard, Piazza, Pinel, & Dehaene, 2005), and it is compressive such that the space between pairs of numbers becomes smaller as numerical magnitude increases (Dehaene & Mehler, 1992; Piazza, Izard, Pinel, LeBihan, & Dehaene, 2004). The present study concerns both aspects of the number line. In particular, we investigate whether individual differences in spatial attentional biases operate similarly for physical lines as well as the mental number line; in addition, we use such attentional biases to investigate whether the mental number line is nonlinearly compressed.

1.1. Spatial organization of number

Evidence for a spatial organization of the mental number line comes from studies demonstrating an association between spatial and numerical information, whereby small numbers (e.g., 1, 2) are associated with the left side of space and larger numbers (e.g., 8, 9) with the right. Dehaene et al. (1993), for example, found that participants asked to make parity (odd/even) judgments were faster to respond to small numbers with the left hand and to larger numbers with the right, the so-called *SNARC* (Spatial-Numerical Association of Response Codes) effect. Similarly, Fischer, Castel, Dodd, and Pratt (2003) found that the presentation of small numbers (centered on a screen) speeded subsequent detection of peripheral stimuli in the left visual field, while the central presentation of larger numbers speeded detection in the right visual field, suggesting that number processing causes shifts in covert spatial attention.

* Corresponding author at: Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London WC1N 3AR, United Kingdom. Tel.: +44 20 7679 1154.
E-mail address: m.longo@ucl.ac.uk (M.R. Longo).

0028-3932/$ – see front matter
doi:10.1016/j.neuropsychologia.2006.11.002

Numerous studies of single-neurons in monkeys (e.g., Nieder, Freedman, & Miller, 2002), neurological patients (e.g., Dehaene & Cohen, 1997), and healthy humans using neuroimaging (e.g., Dehaene, Spelke, Stanescu, Pinel, & Tsivkin, 1999; Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003) and TMS (e.g., Göbel, Calabria, Farnè, & Rossetti, 2006; Oliveri et al., 2004) have demonstrated that numerical tasks involve posterior parietal areas known to be involved in space perception and spatial attention (for review, see Hubbard et al., 2005). Such findings suggest that direction of attention along the mental number line may utilize the same mechanisms involved in the orienting of spatial attention. Indeed, the orientation of attention in other such *representational spaces* (which one imagines, rather than perceives) has been found to activate areas extensively overlapping that involved in spatial attention (Nobre et al., 2004).

Several recent studies provide evidence that patients with hemispatial neglect show similar patterns of attentional bias in numerical, as in physical, space (Priftis, Zorzi, Meneghello, Marenzi, & Umiltà, 2006; Vuilleumier, Ortigue, & Brugger, 2004; Zorzi, Priftis, & Umiltà, 2002). One of the classic tests of neglect is line bisection; patients with neglect typically bisect lines (i.e., mark the perceived center) too far to the right. When required to "bisect" the mental number line, indicating (without calculating) the number midway between two others, these patients display a similar "rightward" bias; that is, they respond with numbers systematically larger than the true midpoint, consistent with the left–right orientation of the mental number line (Zorzi et al., 2002). Importantly, such neglect is specific to numerical processing in that it does not occur when patients bisect other types of ordinal sequences such as months and letters (Zorzi, Priftis, Meneghello, Marenzi, & Umiltà, 2006). Thus, neglect appears both when bisecting physical lines and the mental number line, providing dramatic support for the spatial nature of numerical representation.

While these studies have not found systematic bias on number line bisection in healthy control participants (or brain-damaged patients without neglect), healthy adults have been shown to demonstrate a slight leftward bias on standard line bisection tasks, a phenomenon known as *pseudoneglect* (see Jewell & McCourt, 2000, for review). This bias likely occurs due to the manner in which the parietal lobes of each hemisphere (particularly in and around the intraparietal sulcus) direct attention contralaterally (Corbetta, Shulman, Miezin, & Petersen, 1995). Line bisection (at least when conducted in near space) differentially activates the right parietal lobe (Fierro et al., 2000; Fink et al., 2000), biasing attention leftward and leading to pseudoneglect (Longo & Lourenco, 2006). Importantly, though, consistent individual differences in lateral bias on bisection tasks have been observed (McCourt, 2001), which likely result from stable individual differences in the relative arousal levels of the two hemispheres, termed *characteristic arousal asymmetries* (Kim, Levine, & Kertesz, 1990; Levy, Heller, Banich, & Burton, 1983). The hemispheric asymmetry of electroencephalographic (EEG) activity reported by Morgan, McDonald, and MacDonald (1971), for example, showed a test–retest correlation of .888 (see Levy et al. for review).

There are multiple explanations for the lack of pseudoneglect demonstrated by control participants in the studies described above. Pseudoneglect has been found to decrease in older adults, such as the age-matched controls used in studies of neurological patients (Jewell & McCourt, 2000). Another possibility is that small intervals between numbers (3 and 9) were employed, potentially leading to a ceiling effect on performance. Indeed, using larger numbers (and larger intervals), Göbel et al. (2006) recently demonstrated a "leftward" bias (i.e., responding with numbers that are smaller than the true midpoint value) for number bisection, interpreting this bias as pseudoneglect for the mental number line. However, this study did not compare bias on the number task to bias on the task with physical lines. If the bias towards smaller numbers reflects pseudoneglect of the mental number line, characteristic arousal asymmetries may lead to similar biases on both tasks. A recent study of patients with neglect, however, reported a double-dissociation between neglect for physical lines and for the mental number line (Doricchi, Guariglia, Gasparini, & Tomaiuolo, 2005), suggesting that there may be important differences in the neural representation of space and number. The present study investigated the relation between bias on these two tasks in healthy adults.

1.2. Compression of the mental number line

It has been shown that numerical processing, as with basic sensory modalities, obeys Weber's law such that the discriminability of two numbers decreases as the magnitude of the numbers increases (e.g., Moyer & Landauer, 1967; Restle, 1970), the so-called *numerical size effect*. Two main classes of explanation for this effect have been proposed. Dehaene and colleagues (Dehaene & Mehler, 1992; Piazza et al., 2004) argue that the mental number line is logarithmically compressive, such that as numbers get larger they lie closer to each other. On this account, discriminability decreases with increasing numerical magnitude because the distance between numbers becomes subjectively smaller as their magnitude increases. In contrast, Gallistel and colleagues (Gallistel & Gelman, 1992; Gallistel & Gelman, 2000) argue that number is represented linearly, but becomes more variable as numerical size increases, a property known as *scalar variability* (Whalen, Gallistel, & Gelman, 1999). On this account, numerical representation follows Weber's law, not because larger numbers are subjectively closer, but because their representations overlap more, making them less discriminable.

While recent studies of numerical scaling in both monkey (Nieder & Miller, 2003) and human (Piazza et al., 2004) brains suggest a compressive encoding of number (at least for relatively small numerical magnitudes), existing psychophysical studies in humans do not differentiate between these two theories (Dehaene, 2003). Number "bisection" tasks, however, provide a possible means to address this issue. On the compressive account, a constant leftward attentional bias (pseudoneglect) over the mental number line should lead to a larger leftward numerical bias (i.e., towards smaller numbers) as magnitude increases, since larger numbers are subjectively closer together

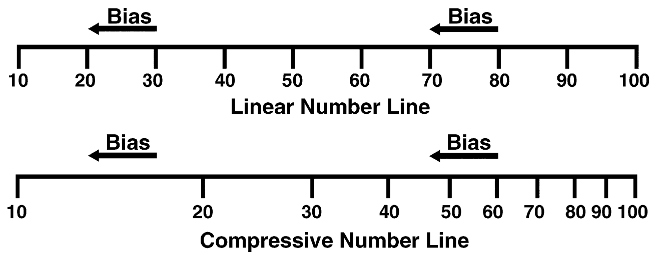

Fig. 1. The effects of bias on linear (top panel) and compressive (bottom panel) number lines. Bias (i.e., pseudoneglect) is represented by the arrows. Note that the length of the arrows is arbitrary and is not meant to indicate specific predictions regarding the magnitude of pseudoneglect. On the linear number line, a constant spatial bias has similar effects at different numerical magnitudes; that is, the right arrow leads to the same numerical bias as the left arrow. In contrast, on the compressive number line, the effects of bias differ depending on the magnitude of the numbers; that is, the right arrow leads to a much larger numerical bias than the left arrow.

(see Fig. 1). On the linear account, in contrast, while the variability of responses may increase with numerical magnitude, responses would be expected to be symmetrically distributed around the true (albeit biased) mean. As a result, while overall *error* may increase with numerical magnitude, directional *bias* would not be expected to change since positive and negative errors should cancel each other out. Thus, if the mental number line is linear, bias should be unrelated to numerical magnitude; if compressive, bias should increase with numerical magnitude.

1.3. The present study

The primary goal of the present study was to examine the relation between direction of attention in physical and numerical space. To this end, participants bisected both physical lines and mental number lines. If the biases observed in these tasks reflect similar mechanisms, participants who are biased farther to the left on physical line bisection should also show more "leftward" bias (i.e., towards smaller numbers) on mental number line bisection. In this study, number pairs were presented with the smaller number either to the left (Experiments 1 and 2) or right (Experiment 2) of the larger number. A secondary goal of the present study was to investigate the spatial organization of the mental number line, in particular, whether it is compressive or linear. If compressive, the numerical magnitude of pseudoneglect should increase as the numbers become larger; if linear, bias should be independent of numerical magnitude.

2. Methods

2.1. Participants

Seventy-six students (42 females, 34 males) between the ages of 18 and 35 participated in these experiments (44 in Experiment 1, 32 in Experiment 2).

2.2. Procedure

2.2.1. Experiment 1

In the first experiment, participants were presented with 80 lines and 80 number pairs, in alternating blocks of 40 trials. Participants bisected lines by making a mark through the perceived center; lengths were randomly selected between 40 and 180 mm. Lines were staggered horizontally across the page so that responses would not be determined by the above response. Number pairs and lines were printed on standard (8.5 in. × 11 in.) sheets of white paper, eight per sheet in portrait orientation. Order of sheets was randomized, and order of blocks was counterbalanced across participants.

Participants "bisected" pairs of numbers by writing the number they estimated to be midway between them. They were told not to explicitly compute the answer, and to go as quickly as they could, using whichever number seemed immediately intuitive, but were not given an explicit time limit. Number pairs were centered on the page, the smaller number on the left, separated by a small horizontal line (2.3 cm) on which the participants wrote their response; 80 pairs of numbers between 11 and 99 were randomly selected. The smaller numbers ranged from 10 to 80 ($M = 35.78$, $SD = 21.38$), and the larger numbers ranged from 21 to 98 ($M = 65.24$, $SD = 22.73$); the difference between the two numbers ranged from 2 to 78 ($M = 29.46$, $SD = 19.45$). There was no correlation between the average of the numbers and the size of the interval between them, $r(79) = .077$.

2.2.2. Experiment 2

In the second experiment, participants bisected 160 numbers pairs, half of which had the smaller number on the left, half the larger number. Order of trials was randomized. As this experiment was designed to control for the spatial relation between the smaller and larger numbers, there was no physical line bisection. Number pairs were selected as in Experiment 1, except that pairs with intervals of less than ten were excluded, due to ceiling effects in performance. The smaller numbers ranged from 10 to 80 ($M = 35.43$, $SD = 19.22$), and the larger numbers ranged from 24 to 99 ($M = 71.64$, $SD = 19.44$); the difference between the two numbers ranged from 11 to 87 ($M = 36.22$, $SD = 19.22$). There was no correlation between the average of the numbers and the size of the interval between them, $r(159) = .013$.

3. Results

3.1. Relation between physical and number line bisection

Significant leftward biases (pseudoneglect) were observed in Experiment 1 both for physical line bisection (.359 mm), $t(43) = 1.74$, $p < .05$ (one-tailed), and number line bisection (.541), $t(43) = -5.31$, $p < .0001$. On the number task, the overall leftward bias is comparable to that (.49) observed by Göbel et al. (2006). Participants were divided into high and low pseudoneglect groups on the basis of a median split on their performance on the physical line bisection task. Significant leftward biases were observed on the number bisection task in both the high (−.740), $t(21) = -5.18$, $p < .0001$, and low (−.341), $t(21) = -2.53$, $p < .02$, pseudoneglect groups (see Fig. 2). This bias was significantly greater, however, in the high pseudoneglect group, $t(42) = 2.87$, $p < .01$. There was also a significant correlation between bias in the two tasks, *Spearman's* $r(43) = .320$, $p < .05$.

Significantly more than half of participants in Experiment 1 showed an overall leftward bias on number line bisection (38 of 44), $p < .0001$, binomial test, and on physical line bisection (28 of 44), $p < .05$, binomial test (one-tailed). Nevertheless, significantly more participants showed an overall leftward bias on number line, than on physical line, bisection, McNemar's $\chi^2(1, N = 44) = 4.50$, $p < .05$. Thus, while bias is significantly correlated between the two tasks, bias on number line bisection appears to be shifted leftward relative to physical line bisection.

In Experiment 1, the smaller number was always on the left, the larger on the right; this procedure may have primed participants to employ a left-to-right orientation of the mental

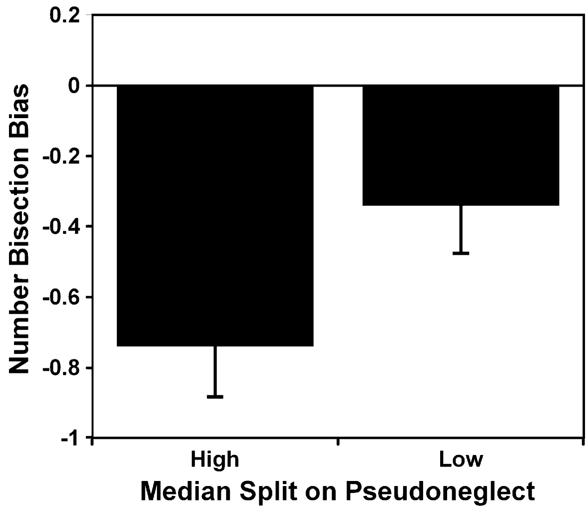

Fig. 2. Bias on mental number line bisection in Experiment 1 for subjects who demonstrated more or less pseudoneglect (i.e., leftward bias) on physical line bisection, as determined by a median split. Participants in the high pseudoneglect group also showed more "leftward" bias when bisecting the mental number line.

number line. Accordingly, in Experiment 2, we presented number pairs counterbalancing whether the smaller or the larger number was on the left. Pseudoneglect was observed in both cases, when the smaller (−.230), $t(31) = -2.32$, $p < .05$, and the larger (−.564), $t(31) = -4.38$, $p < .0001$, numbers were on the left (see Fig. 3). Indeed, while bias in the two conditions was significantly correlated, $r(31) = 0.573$, $p < .001$, participants actually showed *more* pseudoneglect when the larger number was on the left, $t(31) = 3.07$, $p < .005$.

Could the leftward bias observed in number line bisection result from particular kinds of arithmetic strategies participants might employ? That bias on number bisection correlates with bias on physical line bisection argues against this claim; there is no reason to think that spatial attentional biases would relate systematically to numerical estimation strategies likely to lead to leftward bias. Nevertheless, it is worth considering an arithmetic regularity that could, in principle, lead to a leftward bias

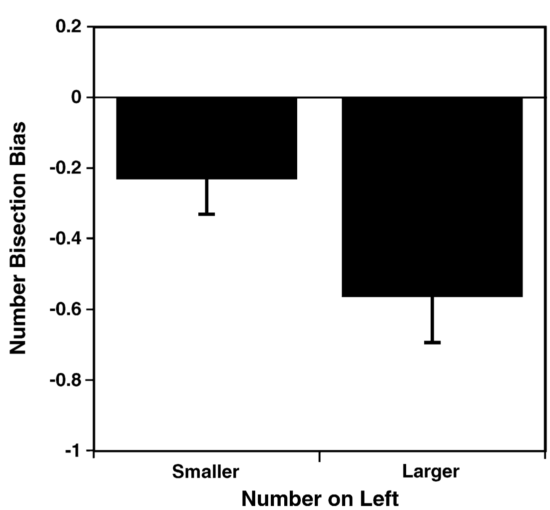

Fig. 3. Bias in Experiment 2 as a function of whether the smaller or larger number was presented on the left on the mental number line bisection task.

on number bisection, namely that responses might be centered on the geometric, rather than the arithmetic mean of the two numbers. Since the geometric mean is always smaller than the arithmetic mean, responses centered around the geometric mean would be smaller than (i.e., to the left of) the arithmetic mean. Could this account for the leftward bias in the present study? Responses were actually significantly larger than the geometric mean in both Experiment 1 (2.93), $t(43) = 26.43$, $p < .0001$, and Experiment 2 (4.09), $t(31) = 37.94$, $p < .0001$. Comparing these values on each trial, this apparent rightward bias from the geometric mean increased in direct proportion to the difference between the geometric and arithmetic means in both Experiment 1, $r(79) = .974$, $p < .0001$, and Experiment 2, $r(159) = .980$, $p < .0001$, suggesting that responses were not systematically biased towards the geometric mean.

3.2. *Effects of numerical magnitude*

To examine effects of magnitude, the mean bias for each number pair was computed and related to the average of the two numbers. There were significant negative correlations between numerical magnitude and rightward bias for the mental number line in both Experiment 1, $r(79) = -.296$, $p < .01$, and Experiment 2, $r(159) = -.388$, $p < .0001$ (see Fig. 4), suggesting that psuedoneglect increased with numerical magnitude. Because observations in the preceding analysis were not independent, coming from the same participants, least-squares regression was used to examine how pseudoneglect changed when the numbers got larger. For each participant, rightward deviation as a percentage of number line length was regressed on the average of the two numbers. The resulting regression slopes in Experiment 1 were significantly negative ($\beta = -.013$), $t(43) = -5.14$, $p < .0001$, again indicating that the magnitude of pseudoneglect increased as numbers got larger. Similar effects were observed in the second experiment, both when the smaller ($\beta = -.030$), $t(31) = -4.12$, $p < .001$, and the larger ($\beta = -0.024$), $t(31) = -4.06$, $p < .001$, number was on the left. This change in bias with increasing numerical magnitude in Experiment 2 was correlated between conditions, $r(31) = .740$, $p < .0001$.

3.3. *Effects of numerical interval size*

To examine effects of numerical interval size, the difference between the two numbers was computed for each number pair and related to mean error and bias for that pair. There were significant increases in overall *error* as the numerical interval size (i.e., difference between two numbers) increased, both in Experiment 1, $r(79) = .924$, $p < .0001$, and in Experiment 2, $r(159) = .864$, $p < .0001$. In contrast, directional *bias* did not appear to be affected by the size of the interval between the two numbers. While there was a significant correlation between interval size and bias in Experiment 1, $r(79) = -.324$, $p < .01$, indicating that leftward bias increased with interval size, this effect appeared to be an artifact of a ceiling effect on performance on trials with very small interval sizes. When the 19 trials with interval size of 10 or less were removed, this effect disappeared, $r(60) = -.107$, *ns*. There was no relation between interval size

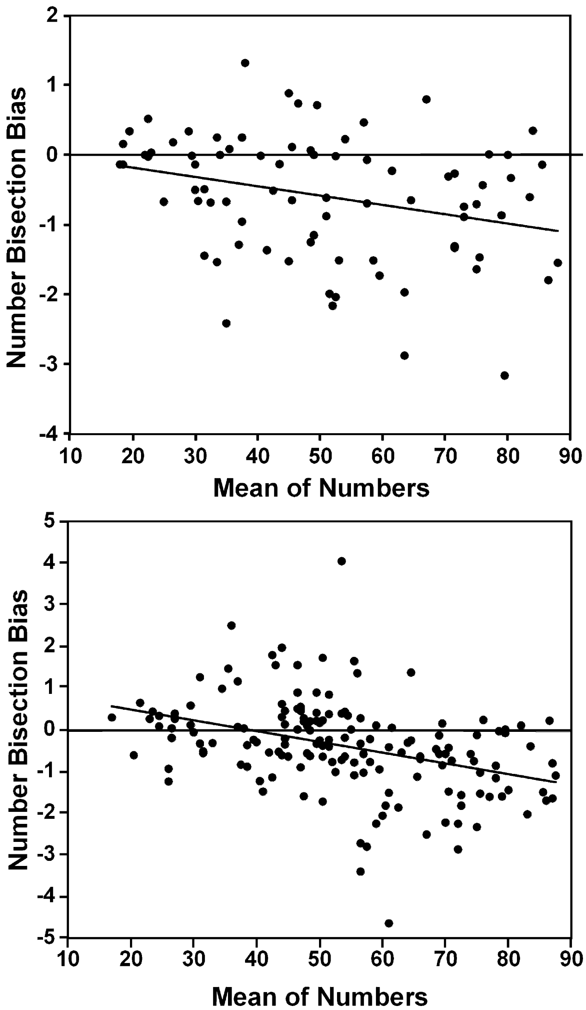

Fig. 4. Bias in Experiment 1 (top panel) and Experiment 2 (bottom panel) as a function of numerical magnitude, calculated as the mean of the two numbers. Leftward bias for mental number line bisection increased with the magnitude of the numbers, suggesting that the mental number line is nonlinearly compressed (see Fig. 1).

and bias in Experiment 2, in which only intervals greater than 10 were used, $r(159) = .134$, *ns*.

An additional analysis examined the effects of line length on physical line bisection in Experiment 1. For each trial, mean bias was computed and compared with line length; there was a marginally significant correlation between line length and pseudoneglect, $r(79) = .191$, $p = .09$. When bias was computed as a proportion of line length, this correlation was eliminated, $r(79) = -.003$, *ns*. As with numerical "length", there were no significant effects of physical line length.

4. Discussion

There are three main findings of the present study. First, the same leftward bias (pseudoneglect) found on standard physical line bisection tasks was also observed when participants bisected the mental number line, consistent with recent findings of Göbel et al. (2006). Second, individual differences in bisection were related between the two tasks; participants who showed stronger leftward bias when bisecting physical lines also showed more bias when bisecting the mental number line. Third, numerical bias increased with the magnitude of the numbers to be bisected.

4.1. Spatial attention and the mental number line

That pseudoneglect was observed on a mental number line bisection task, and was related to bisection of physical lines suggests that spatial attention is oriented along the mental number line in a manner comparable to that on purely spatial tasks. These results generalize the findings of Zorzi et al. (2002) to healthy participants. While a recent study demonstrated that physical and number line bisection can be doubly-dissociated in neglect patients (Doricchi et al., 2005), the present results demonstrate a clear functional relationship between these two tasks in the healthy state. Indeed, Göbel et al. (2006) found that rTMS applied to the right (but not the left) posterior parietal cortex reduced pseudoneglect for the mental number line, analogous to the findings of Fierro et al. (2000) on physical lines. These results support the theory that direction of attention along the mental number line is mediated by the same parietal mechanisms as direction of spatial attention (Hubbard et al., 2005). Furthermore, whereas prior studies of mental number line bisection (e.g., Göbel et al.; Rossetti et al., 2004; Zorzi et al.) presented stimuli auditorily, stimuli in the present study were presented visually, as printed numerals, suggesting that these effects are not tied to any particular sensory modality. More generally, these results demonstrate that pseudoneglect, like hemispatial neglect (Bisiach & Luzzatti, 1978), can occur in representational spaces (even metaphorical ones like the number line).

The relation of bias on both physical and mental number line bisection suggests that characteristic hemispheric attentional asymmetries (cf. Levy et al., 1983) operate similarly in the two tasks. Nevertheless, significantly more participants showed an overall leftward bias in number line, than physical line, bisection, consistent with the suggestion of Göbel et al. (2006) that mental number line bisection is a more sensitive test of pseudoneglect. Thus, even though bias in these tasks is correlated there are nevertheless differences between them, with responses biased farther leftward in number line bisection. This pattern suggests that number bisection may involve additional right parietal processing not involved in physical line bisection. Indeed, numerical comparison has been found to activate regions of the posterior parietal lobe more strongly in the right than the left hemisphere (Chochon, Cohen, van de Moortele, & Dehaene, 1999; Dehaene, 1996; Le Clec'H et al., 2000). Similarly, Knops, Nuerk, Sparing, Foltys, and Willmas (2006) argue for a holistic, or approximate, representation of number in the right parietal lobe. Since the present task requires numerical estimation, it may involve such right parietal areas, potentially accounting for the increased leftward bias observed on number bisection.

An important difference between number and physical line bisection is that it is possible to compute the correct answer in the number line task, unlike physical line bisection. Thus, it is possible that, rather than simply estimating, participants were actually computing the mean of the pairs of numbers. As participants' responses were not timed, there is no way to determine definitively that they were not computing the answers. There is reason, however, to think that participants were, indeed, approximating rather than computing. First, if the network for exact computation were recruited in this task, a rightward – rather than a leftward – bias may have been expected given that precise number representations for exact calculation show a left lateralized pattern of activation (Dehaene et al., 1999). Second, if participants were calculating answers, systematic bias would not be expected at all, nor would such substantial error, in a group of healthy university students. Furthermore, even if bias were to arise via calculation, it would not be expected to correlate with bias on physical line bisection. It is also worth noting that any individual differences in the extent to which responses were computed, rather than estimated, actually work against finding correlations between the two tasks.

In Experiment 2, the leftward bias was significantly greater when the larger number was on the left and the smaller on the right, than vice versa. Importantly, however, biases in the two conditions were significantly correlated. This relation suggests that bias in the two conditions reflect a similar asymmetry in the direction of lateral attention, with an additional leftward constant being added when the larger number is on the right. What might cause the additional constant bias? Participants frequently commented on debriefing that the task was much harder when the larger number was on the left. There is reason, however, to think that increased difficulty would not lead to increased bias. Error (i.e., deviation from the correct answer) was strongly correlated with interval size in both experiments, suggesting that difficulty increased with interval size. Nevertheless, bias (i.e., *directional* deviation from the correct answer) was not significantly related to interval size (see below), suggesting that bias does not increase with increasing difficulty, and is thus unlikely to account for the greater bias when the larger number was on the left. We would suggest another possibility, also motivated by participants' comments on debriefing, that people may mentally shift the smaller number to the left of the larger one before estimating the midpoint. This leftward mental movement may prime attention to be directed farther leftwards, accounting for the increased leftward bias in that condition. This interpretation also provides a possible explanation of the lack of any effect of number order in the studies of Zorzi et al. (2002) and Rossetti et al. (2004), since those studies presented numbers auditorily so that the numbers had a sequential – but not a left/right – order.

Göbel et al. (2006) and Nuerk, Geppert, van Herten, and Willmes (2002), who employed a similar task using forced-choice bisection judgments, both reported an increase in reaction time as interval size increased, suggesting that it is more difficult to bisect larger intervals. While reaction time was not measured in the present study, overall error did increase as the interval size between the two numbers to be bisected increased in both experiments, consistent with the interpretation that task difficulty increases with interval size. There were, however, no apparent effects of interval size on directional *bias*, in contrast to the findings of Göbel et al. and Zorzi et al. (2002). What might account for this difference? Both Göbel et al. and Zorzi et al. used a small number of interval sizes (five and four, respectively), which were held constant, whereas number pairs in the present study were randomly selected meaning that interval size varied freely. Göbel et al. found leftward biases at intervals of 16, 25, 36, and 49, but a rightward bias at interval size 64. This change, however, was not a generally linear rightward shift in bias with increasing interval size; over the range from 16 to 49, no apparent rightward shift is apparent at all. Thus, it is not clear how best to characterize the effect of interval size found by Göbel et al., especially when making predictions about studies (such as the present one) in which interval size varies widely.

4.2. Compression of the mental number line

That the magnitude of pseudoneglect for the mental number line increased as the magnitude of the numbers increased, suggests that the mental number line may be nonlinearly compressed. While linear models employing scalar variability would predict that *error* on number bisection tasks may increase with numerical magnitude, only a compressive account predicts increased *bias*. That is, on the compressive account, a constant attentional bias over the number line should result in larger numerical bias as magnitude increases since numbers lie closer together. This finding dovetails with recent studies of neural tuning curves for number, which are better described by compressed than by linear scales (Nieder & Miller, 2003; Piazza et al., 2004).

Are there alternate explanations of why bias would increase with numerical magnitude? While we have argued that only a compressive account would predict this pattern, another possibility raised by a reviewer is that increasing overlap between numeric representations as magnitude increases may contribute to the increased bias with larger numbers. Both compressive and scalar variability models of the number line propose that the representations of numbers should overlap more as numerical magnitude increases. An increase in representational overlap might lead to an increase in bias if performance was simply more accurate with smaller numbers, which would have the effect of truncating bias for smaller numbers, compared to larger numbers. While we cannot definitively rule out this possibility, two pieces of data argue against such an interpretation. First, such truncation of bias at small magnitudes should apply equally well to neglect patients; those studied by Zorzi et al. (2002), however, showed biases dramatically larger than those observed in the present study, even though the magnitude of numbers bisected was even smaller than those used here. Second, if increased accuracy limits the expression of pseudoneglect at smaller numbers, bias should increase as overall error increases; in contrast, error – but not bias – was strongly related to numerical interval size. Rossetti et al. (2004), furthermore, dissociated error rate from bias; only the latter was improved in neglect patients following prism adaptation. Such findings argue against the interpretation that the relation between bias and numerical magnitude is due to the increased representational overlap of larger, compared to smaller, numbers.

Brannon et al. (2001) argued that the mental number line is linear on the basis of findings they interpreted as evidence that pigeons could perform basic subtraction of small numbers.

Even taking this interpretation at face value, there are several reasons that might account for the apparent discrepancy between their findings and those of the present study. First, as Dehaene (2001) points out, subtraction can be implemented in many types of systems, including those using compressive representations. Second, there may be qualitative differences between avian and human numerical cognition. Third, recent findings have suggested that exact representation of small numbers relies on different mechanisms than approximate representation of larger numbers, the latter system representing the supposed mental number line (Feigenson, Dehaene, & Spelke, 2004a). Exact computation of small numbers, as in Brannon and colleagues' study, therefore, might not utilize compressive representations of number.

Recently, Verguts, Fias, and Stevens (2005) proposed a neural network model of the mental number line which accounts for the size effect in numerical comparison while maintaining linear scaling and constant variability. When the network was trained with numbers matching the observed frequencies reported by Dehaene and Mehler (1992), the weights between number representations and outputs in a comparison task showed compression, accounting for the size effect, but the number representations themselves were not compressed. While this model is not without critics (e.g., Feigenson, Dehaene, & Spelke, 2004b), it is in seeming contradiction to the present interpretation of compressed scaling of the mental number line. Importantly, however, Verguts et al. present their model specifically as incorporating small numbers, up to 15, suggesting that the properties of compressed scaling and scalar variance may hold for larger numbers, such as those used in the present study. Thus, the present interpretation of compression in numbers ranging from 11 to 99 is not directly in contradiction of Verguts and colleagues' model. Given this, their model also provides a potential explanation for why Zorzi et al. (2002), who used smaller numbers than the present study, found no significant effect of numerical magnitude on bias.

In conclusion, the same leftward bias observed in purely spatial bisection tasks was observed for mental number line bisection and, importantly, was greater for participants who showed a greater bias on physical line bisection, suggesting that similar characteristic hemispheric asymmetries in the direction of spatial attention operate in physical and numerical space. Furthermore, this bias increased with the magnitude of the numbers, suggesting that the mental number line is nonlinearly compressed. Thus, the representation of number, a prototypically *abstract* cognitive achievement, appears to be grounded in more basic perceptual and cognitive mechanisms.

Acknowledgements

Portions of the data were previously presented at the annual conference of the Cognitive Neuroscience Society, New York, NY, April 2005. This research was supported by grants from the Psychology Graduate Student Travel and Research Committee at the University of Chicago to both authors, and an NSF graduate research fellowship to MRL. The authors thank Bennett Bertenthal, Janellen Huttenlocher, Larry Hedges, Susan Levine, Jeremy Skipper, Linda Suriyakham, and Pascal Wallisch for helpful discussion, comments, or both.

References

Bisiach, E., & Luzzatti, C. (1978). Unilateral neglect of representational space. *Cortex*, *14*, 129–133.

Brannon, E. M., Wusthoff, C. J., Gallistel, C. R., & Gibbon, J. (2001). Numerical subtraction in the pigeon: Evidence for a linear subjective number scale. *Psychological Science*, *12*, 238–243.

Chochon, F., Cohen, L., van de Moortele, P. F., & Dehaene, S. (1999). Differential contributions of the left and right inferior parietal lobules to number processing. *Journal of Cognitive Neuroscience*, *11*, 617–630.

Corbetta, M., Shulman, G. L., Miezin, F. M., & Petersen, S. E. (1995). Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science*, *270*, 802–805.

Dehaene, S. (1996). The organization of brain activations in number comparison: Event-related potentials and the additive-factors method. *Journal of Cognitive Neuroscience*, *8*, 47–68.

Dehaene, S. (1997). *The number sense*. Oxford: Oxford University Press.

Dehaene, S. (2001). Subtracting pigeons: Logarithmic or linear? *Psychological Science*, *12*, 244–246.

Dehaene, S. (2003). The neural basis of the Weber-Fechner law: A logarithmic mental number line. *Trends in Cognitive Sciences*, *7*, 145–147.

Dehaene, S., Bossini, S., & Giraux, P. (1993). The mental representation of parity and number magnitude. *Journal of Experimental Psychology: General*, *122*, 371–396.

Dehaene, S., & Cohen, L. (1997). Cerebral pathways for calculation: Double dissociation between rote verbal and quantitative knowledge of arithmetic. *Cortex*, *33*, 219–250.

Dehaene, S., & Mehler, J. (1992). Cross-linguistic regularities in the frequency of number words. *Cognition*, *43*, 1–29.

Dehaene, S., Spelke, E., Stanescu, R., Pinel, P., & Tsivkin, S. (1999). Sources of mathematical thinking: Behavioral and brain-imaging evidence. *Science*, *284*, 970–974.

Doricchi, F., Guariglia, P., Gasparini, M., & Tomaiuolo, F. (2005). Dissociation between physical and mental number line bisection in right hemisphere brain damage. *Nature Neuroscience*, *8*, 1663–1665.

Eger, E., Sterzer, P., Russ, M. O., Giraud, A.-L., & Kleinschmidt, A. (2003). A supramodal number representation in human intraparietal cortex. *Neuron*, *37*, 719–725.

Feigenson, L., Dehaene, S., & Spelke, E. (2004a). Core systems of number. *Trends in Cognitive Sciences*, *8*, 307–314.

Feigenson, L., Dehaene, S., & Spelke, E. (2004b). Origins and endpoints of the core systems of number. Reply to Fias and Verguts. *Trends in Cognitive Sciences*, *8*, 448–449.

Fierro, B., Brighina, F., Oliveri, M., Piazza, A., La Bua, V., Buffa, D., et al. (2000). Contralateral neglect induced by right posterior parietal rTMS in healthy subjects. *NeuroReport*, *15*, 1519–1521.

Fink, G. R., Marshall, J. C., Shah, N. J., Weiss, P. H., Halligan, P. W., Grosse-Ruyken, M., et al. (2000). Line bisection judgments implicate right parietal cortex and cerebellum as assessed by fMRI. *Neurology*, *54*, 1324–1331.

Fischer, M. H., Castel, A. D., Dodd, M. D., & Pratt, J. (2003). Perceiving numbers causes spatial shifts of attention. *Nature Neuroscience*, *6*, 555–556.

Gallistel, C. R., & Gelman, R. (1992). Preverbal and verbal counting and computation. *Cognition*, *44*, 43–74.

Gallistel, C. R., & Gelman, R. (2000). Nonverbal numerical cognition: From reals to integers. *Trends in Cognitive Sciences*, *4*, 59–65.

Göbel, S. M., Calabria, M., Farnè, A., & Rossetti, Y. (2006). Parietal rTMS distorts the mental number line: Simulating 'spatial' neglect in healthy subjects. *Neuropsychologia*, *44*, 860–868.

Hubbard, E. M., Piazza, M., Pinel, P., & Dehaene, S. (2005). Interactions between number and space in parietal cortex. *Nature Reviews Neuroscience*, *6*, 435–448.

Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia*, *38*, 93–110.

Kim, H., Levine, S. C., & Kertesz, S. (1990). Are variations among subjects in lateral asymmetry real individual differences or random error in measurement? Putting variability in its place. *Brain and Cognition*, *14*, 220–242.

Knops, A., Nuerk, H.-C., Sparing, R., Foltys, H., & Willmas, K. (2006). On the functional role of human parietal cortex in number processing: How gender mediates the impact of a 'virtual lesion' induced by rTMS. *Neuropsychologia*, *44*, 2270–2283.

Le Clec'H, G., Dehaene, S., Cohen, L., Mehler, J., Dupoux, E., Poline, J. B., et al. (2000). Distinct cortical areas for names of numbers and body parts independent of language and input modality. *NeuroImage*, *12*, 381–391.

Levy, J., Heller, W., Banich, M. T., & Burton, L. A. (1983). Are variations among right-handed individuals in perceptual asymmetries caused by characteristic arousal differences between hemispheres? *Journal of Experimental Psychology: Human Perception and Performance*, *9*, 329–359.

Longo, M. R., & Lourenco, S. F. (2006). On the nature of near space: Effects of tool use and the transition to far space. *Neuropsychologia*, *44*, 977–981.

McCourt, M. E. (2001). Performance consistency of normal observers in forced-choice tachistoscopic visual line bisection. *Neuropsychologia*, *39*, 1065–1076.

Morgan, A. H., McDonald, P. J., & MacDonald, H. (1971). Differences in bilateral alpha activity as a function of experimental task, with a note on lateral eye movements and hypnotizability. *Neuropsychologia*, *9*, 459–469.

Moyer, R. S., & Landauer, T. K. (1967). Time required for judgements of numerical inequality. *Nature*, *215*, 1519–1520.

Nieder, A., Freedman, D. J., & Miller, E. K. (2002). Representation of the quantity of visual items in the primate prefrontal cortex. *Science*, *297*, 1708–1711.

Nieder, A., & Miller, E. K. (2003). Coding of cognitive magnitude: Compressed scaling of numerical information in the primate prefrontal cortex. *Neuron*, *37*, 149–157.

Nobre, A. C., Coull, J. T., Maquet, P., Frith, C. D., Vandenberghe, R., & Mesulam, M.-M. (2004). Orienting attention to locations in perceptual versus mental representations. *Journal of Cognitive Neuroscience*, *16*, 363–373.

Nuerk, H.-C., Geppert, B. E., van Herten, M., & Willmes, K. (2002). On the impact of different number representations in the number bisection task. *Cortex*, *38*, 691–715.

Oliveri, M., Rausei, V., Koch, G., Torriero, S., Turriziani, P., & Caltagirone, C. (2004). Overestimation of numerical distances in the left side of space. *Neurology*, *63*, 2139–2141.

Piazza, M., Izard, V., Pinel, P., LeBihan, D., & Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron*, *44*, 547–555.

Priftis, K., Zorzi, M., Meneghello, F., Marenzi, R., & Umiltà, C. (2006). Explicit versus implicit processing of representational space in neglect: Dissociations in accessing the mental number line. *Journal of Cognitive Neuroscience*, *18*, 680–688.

Restle, F. (1970). Speed of adding and comparing numbers. *Journal of Experimental Psychology*, *83*, 274–278.

Rossetti, Y., Jacquin-Courtois, S., Rode, G., Ota, H., Michel, C., & Boisson, D. (2004). Does action make the link between number and space representation? Visuo-manual adaptation improves number bisection in unilateral neglect. *Psychological Science*, *15*, 426–430.

Verguts, T., Fias, W., & Stevens, M. (2005). A model of exact small-number representation. *Psychonomic Bulletin and Review*, *12*, 66–80.

Vuilleumier, P., Ortigue, S., & Brugger, P. (2004). The number space and neglect. *Cortex*, *40*, 399–410.

Whalen, J., Gallistel, C. R., & Gelman, R. (1999). Nonverbal counting in humans: The psychophysics of number representation. *Psychological Science*, *10*, 130–137.

Zorzi, M., Priftis, K., Meneghello, F., Marenzi, R., & Umiltà, C. (2006). The spatial representation of numerical and nonnumerical sequences: Evidence from neglect. *Neuropsychologia*, *44*, 1061–1067.

Zorzi, M., Priftis, K., & Umiltà, C. (2002). Neglect disrupts the mental number line. *Nature*, *417*, 138–139.